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THE EFFECTS OF LIMITING IONS ON THE ABSORPTION OF NUTRIENTS BY WHEAT

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INTRODUCTION

A partial or complete lack of any one nutrient required by a plant may have considerable effect on the growth and development of that plant. It is reasonable to assume that these changes in growth and development are accompanied by correspondingly definite changes in the internal metabolism of the plant and that such changes may result in, or be reflected in, an altered absorbing power of the plant for other nutrients.

Woodford and McCalla (17) working at this institution in 1934 found that wheat plants growing on a gray wooded soil in which nitrogen and sulphur were low, absorbed a greater amount of phosphorus than did similar plants growing on fertile black loam. These workers concluded from the analysis of the soils that this increased absorption of phosphorus was due to the effect of the low nitrogen supply on the metabolism of the plant rather than to any difference in the availability of phosphorus in the two soils.

These results were checked by the use of carefully controlled water culture experiments and it was found (8) that phosphorus was again absorbed in greater quantities when the nitrogen supply was limited.

The plants were analysed for the six main nutrients in both the above experiments and it was found that a more general conclusion could be drawn, viz., that the high phosphorus content of the plants grown under conditions where nitrogen was limiting probably resulted from influences controlling the anion:cation balance within the plant.

This conclusion was further checked by replicated experiments, which included low calcium cultures, in 1938 (15). The limitation of nitrogen in the culture solutions again resulted in an increased phosphorus absorption, and also caused potassium to be absorbed in smaller amounts. The influence of the calcium limitation was shown by an increased magnesium absorption. Neither the limitation of nitrogen nor the limitation of calcium resulted in a significant variation in the anion:cation ratio.

The experiments reported in this thesis are an extension of the study of the anion:cation balance. The results show the effects of the limitation of nitrogen and potassium, and of potassium and calcium, alone and in combination.

LITERATURE REVIEW

Many workers have studied the effects of the supply of one nutrient on the absorption of other nutrients, and both soil and water cultures have been used.

Soil is normally an infinitely complex medium for the growth of plants and many interactions affecting the solubility and availability of the nutrients may occur within it. For this reason it is difficult to draw any conclusions regarding the absorbing power of a plant from experiments with soil-grown plants unless the elements being studied are very limiting. Even then the conclusions will be confused by the effects of elements not included in the analysis.

Water culture experiments are an excellent means of studying the effects of the supply of one nutrient on the absorption of others and have been used extensively. Few workers in this field have conducted sufficiently complete analyses of the plants to allow a study of the anion:cation ratio to be made, but many of the results presented showing the effects of the supply of one nutrient on the absorption of some one or two other nutrients are entirely compatible with the hypothesis of a constant anion:cation balance.

Lundegardh (7) has found that under conditions of limited potassium supply, an increased absorption of calcium, magnesium and sodium occurred. Under conditions of limited

nitrogen supply, phosphorus absorption was apparently not affected, but potassium absorption was much reduced. Both of these effects would tend to keep the anion:cation balance at a constant level.

Gericke (2) grew wheat seedlings in single salt solutions, supplying all the essential elements by moving the plants from one to another solution. From the growth responses of the plants, it was concluded that nitrate absorption was greatly limited unless potassium was present in the solution.

Beckenbach _et al_ (1) have studied the absorption by corn plants under conditions of varying nutrient concentrations and maintain that: the nitrogen content of the plants was directly related to the potassium and calcium concentrations in the substrate; the potassium content of the plants was inversely related to the nitrate and calcium concentrations in the substrate; and the magnesium content of the plants was directly related to the nitrate and calcium concentrations in the substrate.

Hurd-Karrer (6) has been able to show very definite relations between the absorption of pairs of ions which are chemically similar, such as sulphur and selenium, phosphorus and arsenic, potassium and rubidium, and calcium and strontium. One of the ions in each of these pairs is toxic to plants in relatively low concentrations, but it is possible that such relations may have a more general application.

Nightingale et al (10) have grown tomato plants in solutions low in calcium and nitrogen. The data presented do not include the effects of the nitrate limitation but do show an increased potassium absorption by plants growing in the low calcium solutions. The limitation of calcium did not, however, increase the absorption of magnesium.

Somewhat similar results have been obtained from experiments conducted under a wide range of conditions and by many workers. In general, it appears that the limitation of an anion results in an increased absorption of other anions, or in a decreased absorption of the cations; and that the limitation of a cation results in an increased uptake of the other cations or, more rarely, in a decreased absorption of anions. All of these effects would tend to maintain a relatively constant anion:cation balance.

MATERIALS AND METHODS

The experiments described in this thesis were carried out during the summers of 1939 and 1940. Wheat, variety Red Bobs, was germinated on screens using essentially the method of Hoagland and Broyer (5) except that a nutrient solution rather than distilled water was used in the trays.

While in the single leaf stage, i.e., when from six to eight days old, the seedlings were set out in complete solutions in two-gallon glazed earthenware crocks. Sheet iron lids were perforated with eight holes and corks inserted, the plants being wadded into single holes in the corks with non-absorbent cotton. Seven plants were grown in each two-gallon crock.

A carborundum aerator was inserted through the extra hole in the lid for a short period each day and vigorous aeration carried out. This hole was kept corked except while aeration was in progress.

The young plants were grown in complete solutions for two weeks following transfer from the germination screen. These solutions were then replaced by the experimental solutions and after a further two-week period the plants were collected for analysis.

The crocks were placed in rows of five on the greenhouse bench and the five crocks of each row were treated alike. Tippet's Random Sampling Numbers (16) were used to determine the order of the treatments on the bench.

The solutions used were based on Hoagland's solution, but are only half the strength of the original solution. In 1939, nitrogen and potassium were limited, the limiting solutions containing one-quarter, one-tenth or one-fortieth of the amounts of these elements present in the complete solution. A set of sixteen solutions thus gave all

the possible combinations of these concentrations of nitrogen and potassium. In 1940, potassium and calcium were limited, a similar set of sixteen solutions being used.

The limited nutrients were compensated for by a chemically equivalent amount of another nutrient so that the molar concentration of the solutions did not vary. Nitrogen was compensated for by phosphorus, potassium in 1939 by calcium, and both potassium and calcium in 1940 by magnesium. The composition of these solutions is given in Tables I and II, as millilitres of molar stock solution per litre of culture solution. In addition, each solution received one millilitre of Hoagland's "A-Z" solution (4) per litre, and one millilitre of one-half percent iron tartrate solution per litre every other day.

The limited salts were added in small amounts on alternate days, the amounts shown in Tables I and II being the total amounts added. The plants thus had a limited amount of these nutrients throughout the two-week period rather than a complete lack of them after the solutions became depleted.

Difficulty was anticipated in the 1940 series due to the high concentrations of magnesium developed in the solutions which were low in potassium and calcium. It was found, however, that after three weeks in complete solutions the plants were able to withstand even the highest concentrations of magnesium for the two-week period. Some symptoms

TABLE I

Volume in millilitres of molar stock solution used for each litre of culture solution, 1939

Treatment	KNO_3	$Ca(NO_3)_2$	KH_2PO_4	$MgSO_4$	$Ca(H_2PO_4)_2$*
Complete	2.50	2.50	0.50	1.0	--
1/4 N:Comp.K	1.88	--	1.12	1.0	2.50
1/10 N:Comp.K	0.76	--	2.26	1.0	2.50
1/40 N:Comp.K	.19	--	2.81	1.0	2.50
Comp.N:1/4 K	0.76	3.38	--	1.0	0.26
1/4 N:1/4 K	.76	0.57	--	1.0	3.07
1/10 N:1/4 K	.76	--	--	1.0	3.62
1/40 N:1/4 K	.19	--	0.57	1.0	3.62
Comp.N:1/10 K	0.30	3.60	--	1.0	0.26
1/4 N:1/10 K	.30	0.79	--	1.0	3.07
1/10 N:1/10 K	.30	.22	--	1.0	3.62
1/40 N:1/10 K	.19	--	0.11	1.0	3.86
Comp.N:1/40 K	0.08	3.71	--	1.0	0.26
1/4 N:1/40 K	.08	0.90	--	1.0	3.07
1/10 N:1/40 K	.08	.33	--	1.0	3.62
1/40 N:1/40 K	.08	.06	--	1.0	3.91

* Added as 1/16 molar solution.

TABLE II

Volume in millilitres of molar stock solution used for each litre of culture solution, 1940

Treatment	KNO_3	$Ca(NO_3)_2$	KH_2PO_4	$MgSO_4$	$Mg(NO_3)_2$	$Mg(H_2PO_4)_2$
Complete	2.50	2.50	0.50	1.0	--	--
1/4 K:Comp.Ca	0.16	2.50	0.50	1.0	1.12	--
1/10 K:Comp.Ca	--	2.50	0.30	1.0	1.26	0.10
1/40 K:Comp.Ca	--	2.50	.08	1.0	1.26	.21
Comp.K:1/4 Ca	2.50	0.62	0.50	1.0	1.88	--
1/4 K:1/4 Ca	0.16	.62	.50	1.0	3.00	--
1/10 K:1/4 Ca	--	.62	.30	1.0	3.13	0.10
1/40 K:1/4 Ca	--	.62	.08	1.0	3.13	.21
Comp.K:1/10 Ca	2.50	0.26	0.50	1.0	2.24	--
1/4 K:1/10 Ca	0.16	.26	.50	1.0	3.37	--
1/10 K:1/10 Ca	--	.26	.30	1.0	3.50	0.10
1/40 K:1/10 Ca	--	.26	.08	1.0	3.50	.21
Comp.K:1/40 Ca	2.50	0.07	0.50	1.0	2.43	--
1/4 K:1/40 Ca	0.16	.07	.50	1.0	3.56	--
1/10 K:1/40 Ca	--	.07	.30	1.0	3.69	0.10
1/40 K:1/40 Ca	--	.07	.08	1.0	3.69	.21

of injury did appear but these were considered to be traceable to a deficiency of potassium as much as to an excess of magnesium.

Three series were grown each year and are considered as replicates. Each series was randomized separately so that they were suitable for use in statistical analysis but, since they were grown at different periods during the summer, the variance due to replicate or series is abnormally great.

Chemical Methods

Dry Matters

The complete plants were weighed while fresh, the roots having been freed from excess solution by gentle squeezing by hand. They were then dried in an air-blast oven at 40° to 50°C. until sufficiently dry to grind in a Wiley mill. The remaining moisture was then determined by drying small samples at 105°C. for one hour. The percentage dry matter was calculated from these two results.

Nitrogen

Nitrogen was determined by the reduced iron method of Pucher *et al* (11) to include nitrate nitrogen.

Ash

Samples of approximately two grams were ashed at

600°C. for six hours. The ash was extracted with hot, dilute hydrochloric acid, filtered, and the filtrate made up to a volume of one hundred millilitres. Aliquots of this solution were used for the determination of calcium, magnesium, phosphorus and potassium.

Phosphorus

Phosphorus was precipitated as ammonium phosphomolybdate, dissolved in excess 0.1 N sodium hydroxide and titrated with 0.1 N sulphuric acid, using phenolphthalien as the indicator.

Sulphur

Sulphur was determined by the official A.O.A.C. sodium peroxide method (9).

Potassium

Potassium was precipitated with sodium cobaltinitrite and the precipitate titrated with N/20 potassium permanganate. Details of this procedure are described by Hibbard and Stout (3).

Calcium

Calcium was precipitated as the oxalate and titrated with N/20 potassium permanganate.

Magnesium

Magnesium was determined by a modification of the 8-hydroxyquinoline method of Redmond and Bright (14).

Statistical Method

All of the data were treated statistically by the analysis of variance method. Tables of three series by sixteen treatments (total degrees freedom = 47) were set up and the significance of the variance due to each factor was determined.

REACTION OF THE CULTURE SOLUTION

In 1939 the reaction of the limited nitrogen solutions was distinctly acid, having a pH of approximately 4.0 as compared with a pH of 6.2 for the complete nitrogen solutions. The reaction of these solutions remained relatively constant throughout the two-week period.

In 1940 the reaction of the limited solutions was very close to that of the complete solution. All the solutions had a pH of approximately 6.2 at the beginning and rose to nearly 7.0 at the end of the two-week period.

An attempt was made in 1939 to maintain a complete solution at a pH of 3.5 to 4.0 by adding the necessary amount of phosphoric acid. While not conclusive, the results of this one trial indicated that the reaction of the solution had only a minor influence on absorption over the two-week period. The analyses of the plants from the

acidic complete solution gave results which differed little from those obtained from the analyses of the plants from the neutral complete solution.

The limited solutions, whether they contained 1/4, 1/10 or 1/40 the nitrogen of the complete solution, all had a pH of approximately 4. On the basis of reaction, therefore, the solutions can be divided into only two classes, while in the statistical treatment they were divided into four. The effect of the reaction on absorption would thus tend to mask rather than to increase the significance of the results attributed to nitrogen limitation. The reaction of the nutrient solution cannot be considered a dominant factor influencing absorption in these experiments.

RESULTS, 1939

Dry Weights of Plants

The mean total dry weights of the plants are given in Tables III and the results for the analyses of these data in Table IV.

These results show that the growth of the plants was significantly reduced by the limitation of both nitrogen and potassium during the period when the solutions were limited (two weeks). It had been hoped that the reduction

TABLE III

Mean total dry weight per plant, in grams, for the three 1939 series

Treatment	Series I	Series II	Series III	Average
Complete	0.58	0.56	0.27	0.47
1/4 N:Comp.K	.39	.38	.22	.33
1/10 N:Comp.K	.27	.36	.18	.27
1/40 N:Comp.K	.21	.35	.18	.25
Comp.N:1/4 K	0.55	0.49	0.22	0.42
1/4 N:1/4 K	.26	.36	.19	.27
1/10 N:1/4 K	.24	.29	.18	.24
1/40 N:1/4 K	.19	.28	.18	.22
Comp.N:1/10 K	0.50	0.52	0.25	0.42
1/4 N:1/10 K	.21	.29	.19	.23
1/10 N:1/10 K	.19	.28	.16	.21
1/40 N:1/10 K	.20	.24	.18	.21
Comp.N:1/40 K	0.35	0.40	0.23	0.33
1/4 N:1/40 K	.30	.30	.17	.26
1/10 N:1/40 K	.21	.27	.15	.21
1/40 N:1/40 K	.21	.28	.18	.22

TABLE IV

Results of the analysis of variance of the dry weights per plant results, 1939

Variance due to	D.F.	Mean squares	F value
K treatment	3	0.0127	4.10
N treatment	3	0.0897	28.93
K x N	9	0.0023	0.07
Series	2	0.1037	33.45
Residual	30	0.0031	
Total	47		

1% point, F = 4.51
5% point, F = 2.92

in growth could be made very slight by allowing the plants to grow in complete solutions for an initial period. Since this was not possible, the reduced size of the plants must be considered in discussing the results.

The variation in the size of the plants of the different series is due to the fact that they were grown at different periods during the summer. This variation between series is significant in most cases throughout the results but will not be discussed further since it is of no particular importance in the interpretation of the results.

Percentage Data

The mean percentages of the nutrients in the dry matter are given in Table V and the results of the analysis of variance of these data are given as the mean squares in Table VI.

The increases in the percentages of calcium and magnesium in the dry matter due to potassium limitation are quite definite, but none of the anions shows a significant variation due to this factor. The limitation of nitrogen, on the other hand, caused a decrease in the percentage of calcium and an increase in the percentage of potassium as well as an increase in the percentage of the two anions, phosphorus and sulphur.

TABLE V

Percentage of each nutrient in the dry matter, given as the mean for three 1939 series

Treatment	% N	% P_2O_5	% S	% K	% Ca	% Mg
Complete	4.68	2.85	0.49	7.14	0.57	0.44
1/4 N:Comp.K	4.54	5.90	.56	7.72	.37	.42
1/10 N:Comp.K	4.38	7.28	.64	8.15	.39	.41
1/40 N:Comp.K	4.08	8.45	.76	7.92	.37	.40
Comp.N:1/4 K	4.99	2.66	0.50	6.72	0.63	0.40
1/4 N:1/4 K	4.44	6.22	.62	6.88	.57	.41
1/10 N:1/4 K	4.26	8.39	.63	7.29	.61	.44
1/40 N:1/4 K	4.10	8.54	.72	6.80	.52	.54
Comp.N:1/10 K	4.61	3.11	0.52	4.66	0.86	0.58
1/4 N:1/10 K	4.43	6.84	.66	6.19	.75	.52
1/10 N:1/10 K	4.12	7.63	.67	5.99	.72	.50
1/40 N:1/10 K	3.96	8.10	.71	6.03	.74	.51
Comp.N:1/40 K	4.78	3.47	0.52	3.27	1.02	0.68
1/4 N:1/40 K	4.35	5.55	.61	4.24	0.75	.56
1/10 N:1/40 K	4.12	7.60	.67	4.86	.88	.53
1/40 N:1/40 K	3.96	7.42	.74	4.63	.76	.48

TABLE VI

Results of the analyses of variance of the percentage dry weight values for each nutrient, 1939 series

Variance due to	D.F.	Mean squares for					
		N	K	S	P_2O_5	Ca	Mg
K treatment	3	0.1010	27.5966**	0.0017	0.5864	0.4347**	0.0543**
N treatment	3	1.1721**	2.8856**	0.1070**	64.5324**	0.0751**	0.0063
K x N	9	0.0352	0.2849	0.0022	0.7089	0.0066	0.0102
Series	2	0.5412**	3.2115**	0.1454**	0.6901	0.0987**	0.0537**
Residual	30	0.0695	0.4914	0.0066	0.5079	0.0122	0.0044

** Significant beyond the 1% point

Absorption per Plant Data

Since the growth of the plants was affected by the treatments, it was deemed advisable to study the absorption on a per plant basis. This problem has been discussed by McCalla and Woodford (8).

The mean content in milli-equivalents per plant is presented in Table VII, and the results of the analysis of variance of this data in Table VIII.

As would be expected, these results show that the smaller plants of the low nitrogen treatments contained a smaller amount of most of the nutrients. In the case of phosphorus, however, the increased rate of absorption offset the effect of lesser growth so that a significant increase in the phosphorus content resulted.

Similarly, the somewhat smaller plants of the low potassium treatments contained less of four of the nutrients. The rate of calcium absorption was increased by the potassium limitation to such an extent that an increase in the amount contained per plant resulted. The rate of magnesium absorption was also increased and no decrease in the amount contained per plant occurred. In fact, a slight but not significant increase is apparent.

Although the percentage of potassium in the dry matter increased with the limitation of nitrogen, the

TABLE VII

The average content, in milliequivalents per plant, of each nutrient for the three series, 1939

Treatment	N	P	S	K	Ca	Mg
Complete	1.60	0.18	0.14	0.84	0.13	0.17
1/4 N: Comp.K	1.08	.26	.12	.64	.06	.11
1/10 N:Comp.K	0.87	.26	.11	.56	.05	.09
1/40 N:Comp.K	.71	.28	.12	.48	.04	.08
Comp.N:1/4 K	1.50	0.15	0.13	0.72	0.13	0.14
1/4 N:1/4 K	0.85	.23	.11	.48	.08	.11
1/10 N:1/4 K	.72	.27	.10	.44	.07	.09
1/40 N:1/4 K	.63	.25	.10	.38	.06	.09
Comp.N:1/10 K	1.37	0.18	0.14	0.46	0.18	0.21
1/4 N:1/10 K	0.73	.21	.09	.37	.09	.10
1/10 N:1/10 K	.63	.22	.09	.32	.07	.09
1/40 N:1/10 K	.58	.23	.09	.32	.08	.09
Comp.N:1/40 K	1.11	0.15	0.11	0.26	0.17	0.19
1/4 N:1/40 K	0.80	.19	.10	.27	.10	.12
1/10 N:1/40 K	.62	.22	.08	.25	.09	.09
1/40 N:1/40 K	.63	.26	.10	.26	.08	.09

TABLE VIII

Results of the analyses of variance of milliequivalents per plant, for the 1939 series

Variance due to	D.F.	Mean squares for					
		N	K	S	P	Ca	Mg
K treatment	3	0.1829**	0.3176**	0.0012**	0.0035*	0.0033**	0.0011
N treatment	3	1.4013**	0.1005**	0.0027**	0.0186**	0.0193**	0.0221**
K x N	9	0.0247	0.0168	0.0002	0.0010	0.0003	0.0006
Series	2	1.0134**	0.1426**	0.0173**	0.0377**	0.0051**	0.0199**
Residual	30	0.0342	0.0109	0.0002	0.0009	0.0005	0.0007

* Significant beyond 5% point

** Significant beyond 1% point

milli-equivalents per plant decreased. It is therefore very probable that the increased percentage is due to the reduced growth of the plants and not to an increased absorption of potassium. In a previous experiment (15) it was found that the limitation of nitrogen decreased the potassium absorption, and while such a decrease in potassium absorption is not shown by the results of this experiment the data are not contrary to the conclusions reached at that time. This question is dealt with more thoroughly in the discussion.

The decrease in calcium absorption when nitrogen was limited is shown both by the percentage and the milli-equivalents per plant and cannot be entirely due to the decreased growth of the plants.

Ion Ratios

The ratios of the limited ions to each of the other ions were calculated from the milli-equivalents per plant data. The mean values for these ratios are presented in Table IX, and the results of the analysis of variance in Table X.

The decreases in the N:P and N:S ratios when nitrogen was limited are due partly to an increase in the phosphorus and sulphur contents and partly to a decrease

in the nitrogen content of the plants. The decreased nitrogen content has also resulted in a decrease in the N:K ratio. The decreases in the K:P and K:S ratios are largely due to the increased phosphorus and sulphur content, and the increases in the K:Ca and K:Mg ratios are due to the decreased calcium and magnesium content of the plants. Potassium content was decreased slightly but probably not sufficiently to affect any of the ratios significantly.

The decreases in the N:Ca and N:Mg ratios when potassium was limited are apparently due to the increased calcium and magnesium content as the nitrogen content was only slightly reduced. This increase in the magnesium content of the plants was insufficient to be significant in the analysis of the milli-equivalents per plant, but is probably quite real, nevertheless.

The decreases in the K:N, K:P, K:S, K:Ca and K:Mg ratios when potassium was limited are largely due to the decreased potassium content of the plants. The analyses of the milli-equivalents per plant show a decrease in the nitrogen, phosphorus and sulphur content, but the potassium content was decreased so greatly that these ratios are also decreased. The increased calcium and magnesium contents contribute to the decreases shown by the K:Ca and K:Mg ratios. The increased N:K ratio is due to the decreased potassium content, the decrease in the nitrogen content being small in comparison.

TABLE IX

The average ratios, calculated from the milliequivalents per plant data, of the limited to the other nutrients
1939

Treatment	N:K	N:P	N:S	N:Ca	N:Mg	K:N	K:P	K:S	K:Ca	K:Mg
Complete	1.84	8.93	11.10	11.78	9.07	0.55	4.74	6.02	6.43	4.96
1/4 N:Comp.K	1.65	4.14	9.10	16.73	9.50	.61	2.49	5.62	10.10	5.76
1/10 N:Comp.K	1.53	3.26	8.28	16.12	9.58	.65	2.12	5.45	10.47	6.25
1/40 N:Comp.K	1.45	2.56	6.32	16.63	8.84	.70	1.97	4.40	11.40	6.12
Comp.N:1/4 K	2.06	9.92	11.48	11.44	10.13	.49	4.83	5.58	5.58	4.92
1/4 N:1/4 K	1.80	3.83	8.11	11.34	8.10	.56	2.13	4.50	6.33	4.53
1/10 N:1/4 K	1.64	2.68	7.68	9.74	8.13	.61	1.64	4.68	5.94	4.96
1/40 N:1/4 K	1.68	2.53	6.92	11.15	7.15	.59	1.51	4.12	6.67	4.26
Comp.N:1/10 K	3.01	7.70	10.02	7.73	7.01	.35	2.77	3.57	2.77	2.63
1/4 N:1/10 K	1.99	3.40	7.82	8.34	7.61	.50	1.72	3.97	4.22	3.87
1/10 N:1/10 K	1.97	2.90	7.38	8.53	7.37	.51	1.47	3.77	4.38	3.75
1/40 N:1/10 K	1.83	2.55	6.60	7.92	6.79	.55	1.39	3.65	4.39	3.74
Comp.N:1/40 K	4.36	7.28	10.39	6.70	6.11	.24	1.77	2.51	1.62	1.51
1/4 N:1/40 K	2.96	4.17	8.10	8.51	6.68	.35	1.43	2.88	2.85	2.40
1/10 N:1/40 K	2.42	2.84	7.44	7.60	6.58	.42	1.18	3.11	3.12	2.74
1/40 N:1/40 K	2.29	2.82	6.14	7.59	7.00	.42	1.18	2.61	3.15	2.95

TABLE X

Results of the analyses of variance for the ratios of the limited to other nutrients, 1939

Variance due to	D.F.	Mean squares for				
		N:P	N:S	N:K	N:Ca	N:Mg
K treatment	3	1.1404	1.6754	4.8681**	149.5753**	16.9627**
N treatment	3	88.3294**	38.4545**	2.4230**	7.3154	0.9448
K x N	9	0.1561	0.4813	0.3863	4.5226	1.6483
Series	2	0.9049	6.8794**	1.1440**	32.7644**	4.6239*
Residual	30	0.4156	0.8069	0.1382	4.3632	1.1890
		K:N	K:P	K:S	K:Ca	K:Mg
K treatment	3	0.1637**	5.1144**	15.5072**	110.1308**	25.4668**
N treatment	3	0.0585**	10.5908**	1.1952**	12.4555**	1.9572**
K x N	9	0.0017	1.0623**	0.5626	1.9805	0.5346
Series	2	0.0308**	0.1361	7.4952**	3.5154	3.8508**
Residual	30	0.0027	0.1637	0.2135	1.6426	0.3467

* Significant beyond the 5% point

** Significant beyond the 1% point

Correlation Coefficients

Various correlation coefficients involving combinations of the percentage results are presented in Table XI.

TABLE XI

Correlation coefficients for the percentages of various nutrients

Correlation	Value	Correlation	Value
r_{KCa}	-.92**	r_{NP}	-.88**
r_{KMg}	-.86**	r_{NS}	-.91**
r_{CaMg}	.82**	r_{PS}	.92**
$r_{KCa.Mg}$	-.73**	$r_{NP.S}$	-.27
$r_{KMg.Ca}$	-.52*	$r_{NS.P}$	-.54*
$r_{CaMg.K}$	.15	$r_{PS.N}$	.60*
$R_{K.CaMg}$	.94**	$R_{N.PS}$	.92**

* Significant beyond the 5% point

** Significant beyond the 1% point

These correlations were calculated on the treatment totals rather than on the individual pairs as the large variations between series tended to result in a grouping of the values. Analyses of covariance showed

that the regression within groups was very significantly different from the regression between groups. Individual data cannot, therefore, be used in a single correlation analysis.

These correlations verify the conclusion that the limitation of potassium led to an increase in the absorption of calcium and of magnesium. The high positive correlation between calcium and magnesium is largely due to the similar effect of potassium limitation on each of them and disappears when the effect of potassium is eliminated. The multiple correlation coefficient is not significantly larger than the simple correlation coefficients, indicating that the same factor influences the absorption of calcium and magnesium.

The interpretation of the correlations between anions is similar. Nitrogen limitation had a similar effect on the absorption of phosphorus and of sulphur, and a positive correlation between these two ions results. This correlation coefficient is much lower when the effect of nitrogen is eliminated but is still significant, and probably indicates a similar action of external factors on the absorption of these two nutrients. A positive correlation between pairs of nutrients would result if the plants were all grown in complete solutions but subjected to differences in growing conditions as most environmental conditions affect the absorption of all elements somewhat

similarly. It is this tendency toward a positive correlation due to the environmental conditions that makes the individual data unsuitable for calculating correlation coefficients.

The partial coefficients for correlations between potassium and calcium absorption, and between potassium and magnesium absorption are lower than the corresponding simple correlation coefficients. It is biologically impossible to limit the potassium supply without affecting the absorption of both calcium and magnesium, so these partial correlation coefficients represent a statistical consideration only and cannot be given a biological interpretation.

Similarly the partial coefficients for correlations between nitrogen and phosphorus, and between nitrogen and sulphur are not biologically significant as nitrogen is the only independent variable and both phosphorus and sulphur absorption increase whenever nitrogen is limited.

RESULTS, 1940

Dry Weights of Plants

The mean dry weights of the plants are presented in Table XII, and the results of the analysis of variance of these results in Table XIII.

The variations between series are high as in 1939 and are again due to differences in the environmental conditions as the series were grown at different periods throughout the summer.

These results show that during the two-week period, while the plants were in limited solutions, the reduction in growth due to calcium limitation was not great enough to be significant. It is very probable that a significant reduction in growth would have occurred had the plants been grown in low calcium solutions for a longer period. The limitation of potassium even for the two-week period was sufficient to reduce the growth of the plants, as was the case in 1939.

TABLE XII

Mean total dry weight per plant, in grams, for the three 1940 series

Treatment	Series I	Series II	Series III	Average
Complete	1.23	0.88	0.44	0.85
1/4 K:Comp.Ca	1.23	.67	.53	.81
1/10 K:Comp.Ca	1.00	.61	.39	.67
1/40 K:Comp.Ca	1.07	.64	.37	.69
Comp.K:1/4 Ca	1.46	0.69	0.45	0.87
1/4 K:1/4 Ca	1.13	.65	.44	.74
1/10 K:1/4 Ca	1.26	.77	.37	.80
1/40 K:1/4 Ca	1.22	.66	.31	.73
Comp.K:1/10 Ca	1.30	0.89	0.44	0.88
1/4 K:1/10 Ca	1.45	.85	.45	.92
1/10 K:1/10 Ca	1.15	.73	.36	.75
1/40 K:1/10 Ca	0.96	.53	.27	.59
Comp.K:1/40 Ca	1.35	0.82	0.41	0.86
1/4 K:1/40 Ca	1.10	.61	.34	.68
1/10 K:1/40 Ca	1.15	.70	.32	.72
1/40 K:1/40 Ca	0.98	.46	.28	.57

TABLE XIII

Results of the analysis of variance of the dry weights per plant results, 1940

Variance due to	D.F.	Mean squares	F value
K treatment	3	0.1004	17.31
Ca treatment	3	0.0142	2.45
K x Ca	9	0.0146	2.52
Series	2	2.6316	453.72
Residual	30	0.0058	
Total	47		

1% point, F = 4.51
5% point, F = 2.92

Percentage Data

The mean percentages of the nutrients in the dry matter are presented in Table XIV and the results of the analysis of variance of these results in Table XV.

The limitation of either potassium or calcium resulted in an increased percentage of the other cation, magnesium, in the dry matter. The anion absorption was also affected by the limitation of these two cations, the percentage nitrogen being reduced by potassium limitation and the percentage nitrogen and phosphorus being reduced by calcium limitation. The effect of potassium limitation on phosphorus absorption was affected by the calcium level and the interaction between the treatments is significant in this one case.

TABLE XIV

Percentage of each nutrient in the dry matter,
given as the mean for three 1940 series

Treatment	% N	% P_2O_5	% S	% K	% Ca	% Mg
Complete	5.04	2.75	0.42	6.76	0.53	0.32
1/4 K:Comp.Ca	5.01	2.79	.45	5.61	.55	.44
1/10 K:Comp.Ca	4.91	2.97	.46	3.98	.58	.59
1/40 K:Comp.Ca	4.74	3.31	.48	2.70	.67	.64
Comp.K:1/4 Ca	4.99	2.74	0.42	6.30	0.24	0.52
1/4 K:1/4 Ca	4.90	2.89	.47	5.40	.22	.61
1/10 K:1/4 Ca	4.51	2.51	.44	3.70	.23	.71
1/40 K:1/4 Ca	4.30	2.55	.43	2.61	.25	.76
Comp.K:1/10 Ca	4.79	2.71	0.44	6.11	0.19	0.56
1/4 K:1/10 Ca	4.58	2.44	.43	4.83	.16	.68
1/10 K:1/10 Ca	4.47	2.30	.45	3.93	.20	.78
1/40 K:1/10 Ca	4.26	2.44	.43	2.90	.18	.81
Comp.K:1/40 Ca	4.61	2.61	0.43	5.94	0.14	0.57
1/4 K:1/40 Ca	4.58	2.55	.46	5.28	.14	.68
1/10 K:1/40 Ca	4.38	2.20	.40	3.96	.17	.69
1/40 K:1/40 Ca	4.23	2.30	.44	3.14	.17	.74

TABLE XV

Results of the analyses of variance of the percentage dry weight values for each nutrient, 1940 series

Variance due to	D.F.	Mean squares for					
		K	Ca	Mg	N	P_2O_5	S
K treatment	3	27.5462**	0.0057	0.1378**	0.5310**	0.1012	0.0013
Ca treatment	3	0.2293	0.4713**	0.1057**	0.5278**	0.7139**	0.0010
K x Ca	9	0.1602	0.0018	0.0039	0.0246	0.1317*	0.0012
Series	2	11.6253**	0.0442**	0.0073	0.7585**	0.1459*	0.0042*
Residual	30	0.2138	0.0025	0.0064	0.0241	0.0427	0.0013

* Significant beyond the 5% point

** Significant beyond the 1% point

Absorption per Plant Data

The mean content per plant for all three series is given in milli-equivalents in Table XVI, and the results of the analyses of variance of these results, in Table XVII.

The limitation of potassium in the solutions resulted in a decreased growth of the plants and, hence, the milli-equivalents per plant of nitrogen, phosphorus and sulphur, as well as of potassium, were reduced. The increased absorption of calcium and magnesium was sufficient to offset this effect and the milli-equivalents per plant did not vary significantly.

The limitation of calcium in the solution for two weeks did not significantly affect the dry weights of the plants but it did decrease the amounts of calcium, nitrogen and phosphorus absorbed by the plants. The increased absorption of magnesium resulted in a higher magnesium content per plant.

TABLE XVI

The average content, in milliequivalents per plant, of each nutrient for the three series, 1940

Treatment	N	P	S	K	Ca	Mg
Complete	3.01	0.32	0.22	1.43	0.23	0.22
1/4 K:Comp.Ca	2.85	.31	.23	1.11	.24	.31
1/10 K:Comp.Ca	2.29	.27	.19	0.62	.20	.32
1/40 K:Comp.Ca	2.29	.30	.20	.44	.23	.34
Comp.K:1/4 Ca	3.02	0.32	0.22	1.35	0.11	0.37
1/4 K:1/4 Ca	2.56	.30	.22	0.97	.09	.38
1/10 K:1/4 Ca	2.52	.27	.22	.65	.10	.46
1/40 K:1/4 Ca	2.16	.24	.20	.43	.10	.44
Comp.K:1/10 Ca	2.97	0.34	0.23	1.34	0.09	0.39
1/4 K:1/10 Ca	2.97	.30	.25	1.04	.08	.52
1/10 K:1/10 Ca	2.35	.23	.21	0.66	.08	.50
1/40 K:1/10 Ca	1.74	.20	.16	.38	.06	.41
Comp.K:1/40 Ca	2.83	0.31	0.23	1.30	0.07	0.40
1/4 K:1/40 Ca	2.23	.24	.22	0.88	.06	.39
1/10 K:1/40 Ca	2.21	.22	.19	.63	.07	.44
1/40 K:1/40 Ca	1.70	.21	.17	.40	.06	.38

TABLE XVII

Results of the analyses of variance of milliequivalents per plant, for the 1940 series

Variance due to	D.F.	Mean squares for					
		K	Ca	Mg	N	P	S
K treatment	3	2.0441**	0.0004	0.0142	2.1394**	0.0154**	0.0055**
Ca treatment	3	0.0181	0.0631**	0.0534**	0.3205**	0.0063**	0.0005
K x Ca	9	0.0072	0.0004	0.0045	0.1120	0.0031	0.0007
Series	2	1.4981**	0.0914**	0.6802**	24.0531**	0.3188**	0.2093**
Residual	30	0.0155	0.0011	0.0052	0.0703	0.0011	0.0005

** Significant beyond 1% point

Ion Ratios

The mean values for the ratios of nitrogen and potassium to the other nutrients are given in Table XVIII, and the results of the analyses of variance of these results in Table XIX.

The limitation of potassium in the solutions resulted in a lower potassium content per plant and all the ratios in which potassium is the numerator are, therefore, decreased. Potassium limitation also resulted in a decrease in the milli-equivalents of nitrogen per plant and so the N:S and N:Mg ratios are also decreased. The variability of the N:P and N:Ca ratios is great and the effect of the reduced nitrogen content per plant on these ratios is not significant.

The calcium content per plant was decreased by the limitation of calcium in the solutions and this resulted in an increase in the K:Ca and N:Ca ratios. The calcium treatments also had a significant effect on the N:Mg and K:Mg ratios due to the increased magnesium and decreased nitrogen absorption.

TABLE XVIII

The average ratios, calculated from the milliequivalents per plant data, of nitrogen and potassium to the other nutrients, 1940

Treatment	N:K	N:P	N:S	N:Ca	N:Mg	K:N	K:P	K:S	K:Ca	K:Mg
Complete	2.09	9.49	13.38	14.04	13.53	0.48	4.56	6.41	6.77	6.48
1/4 K:Comp.Ca	2.52	9.54	12.83	13.64	10.23	.41	3.85	5.22	5.58	4.17
1/10 K:Comp.Ca	3.59	8.75	12.06	12.61	7.18	.29	2.54	3.46	3.74	2.08
1/40 K:Comp.Ca	5.05	7.54	11.48	10.47	6.59	.20	1.52	2.34	2.09	1.32
Comp.K:1/4 Ca	2.22	9.50	13.57	29.70	8.19	0.45	4.29	6.12	13.45	3.70
1/4 K:1/4 Ca	2.56	8.88	11.64	35.57	6.90	.39	3.53	4.60	14.44	2.73
1/10 K:1/4 Ca	3.68	9.37	11.70	29.96	5.54	.29	2.69	3.38	9.28	1.60
1/40 K:1/4 Ca	4.81	8.99	11.56	24.58	4.86	.22	1.93	2.54	5.54	1.04
Comp.K:1/10 Ca	2.19	8.98	12.43	35.07	7.38	0.46	4.12	5.69	16.18	3.37
1/4 K:1/10 Ca	2,74	9.82	12.03	39.16	5.74	.38	3.72	4.56	16.64	2.17
1/10 K:1/10 Ca	3.39	10.22	11.52	31.40	4.95	.31	3.24	3.67	10.35	1.60
1/40 K:1/10 Ca	4.36	8.79	11.66	32.96	4.57	.24	2.12	2.90	8.43	1.14
Comp.K:1/40 Ca	2.17	9.28	12.29	45.50	6.88	0.46	4.29	5.67	20.57	3.18
1/4 K:1/40 Ca	2.46	9.42	10.64	60.53	5.81	.41	3.88	4.42	25.77	2.40
1/10 K:1/40 Ca	3.33	10.40	12.46	39.37	5.59	.32	3.35	4.06	13.28	1.85
1/40 K:1/40 Ca	3.98	8.77	11.04	49.28	5.06	.26	2.35	3.02	14.39	1.39

TABLE XIX

Results of the analyses of variance for the ratios of nitrogen and potassium to the other nutrients, 1940

Variance due to	D.F.	Mean squares for				
		N:P	N:S	N:K	N:Ca	N:Mg
K treatment	3	2.9857	4.8544**	13.5537**	190.9000	33.1236**
Ca treatment	3	1.0682	1.4511	0.2946	2643.8406**	36.3349**
K x Ca	9	0.8847	1.0101	0.1713	49.5958	3.4971*
Series	2	6.4759**	6.3689**	6.2730**	1801.0167**	2.0158
Residual	30	1.0263	0.8916	0.2263	170.3598	0.9699
		K:N	K:P	K:S	K:Ca	K:Mg
K treatment	3	0.1250**	12.3270**	23.7636**	179.3673**	20.4305**
Ca treatment	3	0.0016	0.3490	0.0949	399.6941**	5.3974**
KxCa	9	0.0008	0.2252	0.4133	11.9785	0.9253
Series	2	0.0408*	7.1381*	7.7092**	476.4767**	2.7069**
Residual	30	0.0010	0.1634	0.3249	30.2958	0.3989

* Significant beyond 5% point

** Significant beyond 1% point

Correlation Coefficients

Various correlation coefficients for combinations of the percentage data are shown in Table XX.

TABLE XX

Correlation coefficients for the percentages of various nutrients

Correlation	Value	Correlation	Value
r_{KCa}	-.03	r_{KN}	.72**
r_{KMg}	-.79**	r_{KP}	.15
r_{CaMg}	-.54*	r_{NP}	.70**
$r_{KCa.Mg}$	-.88**	$r_{KN.P}$	.87**
$r_{KMg.Ca}$	-.96**	$r_{KP.N}$	-.71**
$r_{CaMg.K}$	-.92**	$r_{NP.K}$	.86**
$R_{K.CaMg}$	.96**	$R_{K.NP}$	.95**

* Significant beyond the 5% point

** Significant beyond the 1% point

These correlation coefficients were calculated on the treatment totals as were those for the 1939 data.

Two cations were limited in these experiments and so a negative correlation occurs with any pair of cations, but since both potassium and calcium were limited

in many of the solutions the normal effect of one on the absorption of the other was obscured. The partial correlation coefficients are higher than the corresponding simple correlation coefficients, especially in the case of the correlation between potassium and calcium, but these increases probably have little biological significance since the limitation of one of these elements affects the absorption of both the others.

The high positive coefficient for the correlation between potassium and nitrogen absorption is considered in the discussion. The correlation between nitrogen and phosphorus may be due partly to the variations caused by environmental factors and partly to a similar effect of potassium limitation on both of them, although the correlation between potassium and phosphorus is not significant. An analysis of covariance will be necessary before these data can be interpreted completely.

THE ANION:CATION RATIOS

The ratios of the total anions to the total cations per plant (i.e. N + P + S : K + Ca + Mg) were determined and analysed statistically. The mean values of these ratios are given, for each year, in Table XXI, and the mean squares for the analyses of variance in Table XXII.

Neither the limitation of the nitrogen in 1939, nor of calcium in 1940 had a significant effect on this

anion:cation ratio. The limitation of potassium resulted in an increase in this ratio in both years but the increase was not proportional to the decided decrease in the potassium content of the plants.

TABLE XXI

Mean values, for three series, of the anion:cation ratios

1939		1940	
Treatment	Ratio	Treatment	Ratio
Complete	1.63	Complete	1.89
1/4 N:Comp.K	1.76	1/4 K:Comp.Ca	2.04
1/10 N:Comp.K	1.74	1/10 K:Comp.Ca	2.36
1/40 N:Comp.K	1.79	1/40 K:Comp.Ca	2.70
Comp.N:1/4 K	1.74	Comp.K:1/4 Ca	1.94
1/4 N:1/4 K	1.81	1/4 K:1/4 Ca	2.10
1/10 N:1/4 K	1.80	1/10 K:1/4 Ca	2.39
1/40 N:1/4 K	1.86	1/40 K:1/4 Ca	2.60
Comp.N:1/10 K	1.96	Comp.K:1/10 Ca	1.92
1/4 N:1/10 K	1.87	1/4 K:1/10 Ca	2.07
1/10 N:1/10 K	1.94	1/10 K:1/10 Ca	2.17
1/40 N:1/10 K	1.93	1/40 K:1/10 Ca	2.37
Comp.N:1/40 K	2.22	Comp.K:1/40 Ca	1.89
1/4 N:1/40 K	2.21	1/4 K:1/40 Ca	1.99
1/10 N:1/40 K	2.10	1/10 K:1/40 Ca	2.24
1/40 N:1/40 K	2.20	1/40 K:1/40 Ca	2.45

TABLE XXII

Mean squares for the analyses of variance of the anion:cation ratios for both years

Variance due to	D.F.	Mean squares	
		1939	1940
N limitation	3	0.0049	--
K limitation	3	0.4750**	0.8968**
Ca limitation	3	--	0.0551
N x K interaction	9	0.0313	--
K x Ca interaction	9	--	0.0177
Series	2	0.2415**	0.4973**
Residual	30	0.0071	0.0197

** Significant beyond 1% point

DISCUSSION

The data presented in this paper show that the limitation of one nutrient may, under these conditions, have a marked effect on the absorption of other nutrients. It has been suggested by workers at this institution (8) that these effects are due, in part at least, to an attempt on the part of the plant to maintain a constant anion: cation balance within itself.

The anion:cation balance within a plant may be maintained, when some nutrient is limited, either by an increased absorption of like ions or by a decreased absorption of ions of the opposite charge, or by both of these means operating together. The author believes that most of the results presented in this paper can be explained on this basis.

In the 1939 experiments the limitation of nitrogen resulted in an increase in the percentages of both the other anions, phosphorus and sulphur. The absorption of phosphorus was increased to such an extent that the total phosphorus per plant increased in spite of the marked decrease in the growth of the plants. The limited amount of nitrogen supplied to these plants also resulted in a decreased total absorption of calcium and magnesium, although the reduction in the growth of the plants was sufficient to

keep the percentage of these nutrients in the dry matter relatively constant. The increases in the K:Ca and K:Mg ratios due to nitrogen limitation are a further indication of the decreased absorption of these two nutrients.

In the 1940 experiments the limitation of calcium caused the plants to absorb more magnesium and less nitrogen and phosphorus. These results are shown both by the percentages of these nutrients in the dry matter and by the milli-equivalents per plant, and also by the lowering of the N:Mg ratio.

The effects of the limitation of potassium, in both years, can be explained on the same basis although in this case the constant anion:cation balance was not maintained. In the 1939 experiments the absorption of both calcium and magnesium was increased by potassium limitation although the increase in magnesium absorption is slight and is significant only for the percentage data. In the 1940 experiments the limitation of potassium resulted in an increase in the percentage of magnesium and a decrease in the percentage of phosphorus in the dry matter, and in a decrease in both the percentage and total nitrogen absorption.

The failure of the plants to absorb anions and cations in a constant ratio when potassium was limited indicates that anion absorption is more independent of cations than cation absorption is of anions. It is probable

that the constant anion:cation balance is maintained in the plant so that no accumulation of charge occurs, but that the phenomenon of ion exchange favors anion absorption so that the ratio is not one to one. Thus, the exchange of bicarbonate or other negative ions for a nutrient anion allows absorption of these anions independently without the accumulation of a charge. When potassium is limited it is apparently possible for the proportion of absorption taking place by means of ion exchange to increase and so the anion:cation ratio also increases. The fact that the limitation of potassium did decrease nitrogen absorption indicates that this increase in the amount of ion exchange occurring does not take place readily, or that it can occur only to a limited extent.

There is no cation which is commonly excreted from the roots as is the bicarbonate ion, and so cation absorption by means of ion exchange cannot occur. When the supply of an anion is limited cation absorption cannot continue in excess of anion absorption without the accumulation of a charge and is therefore curtailed. The anion:cation ratio is thus maintained at a relatively constant level.

It is interesting to note that the unsuitability of the ammonium ion as a nutrient may be related to this phenomenon. If nitrogen is absorbed as a cation the anion:cation ratio would tend to become less than one; but this

is not possible without an exchange of cations. The absorption of the cations would, therefore, be limited by the amount of the anions, phosphorus and sulphur, which could be absorbed. Under these conditions it is conceivable that the absorption of the cations, especially of ammonia and potassium, might be so curtailed that the development of the plant would be hindered.

Throughout these experiments two nutrients have been limited concurrently and hence the effects of the limitation of one of these on the absorption of the other are obscured. Thus the increased absorption of calcium due to potassium limitation occurred only in 1939, and did not occur in 1940 when many of the solutions had only a limited calcium supply. Similarly the decreased absorption of nitrogen when potassium was limited is shown by the data only when one of these nutrients was limited in the solutions and is not shown by the 1939 results.

In almost every case, the effect of one limited ion was independent of the amount of the other limited ion present in the solutions. In the analysis of the K:P ratio (Table X), the N:Mg ratio (Table XIX), and of the percentage P_2O_5 (Table XV), however, the interactions are significant. The ratios were calculated on the milli-equivalents per plant and, as is shown by Table VIII, potassium limitation decreased the phosphorus content per plant though the effect was much smaller than the increase due to nitrogen limitation.

Hence, the effect of potassium on the K:P ratio was less when phosphorus was high due to the low nitrogen supply. The interaction shown by the N:Mg ratio can be explained similarly as the limitation of potassium affected the nitrogen content of the plants to a much greater extent than did the limitation of calcium. The interaction between potassium and calcium treatments on the percentage phosphorus can be attributed to the high figures for the 1/10 K: Complete Ca and 1/40 K: Complete Ca solutions (Table XIV) and is probably not significant from a biological point of view.

The correlation coefficients between the percentages of nitrogen and potassium in the dry matter were particularly high if only one of these nutrients was limited. It is possible that some direct relation between the absorption of these two nutrients exists, as suggested by Gericke (2). It seems more probable, however, that this close correlation between nitrogen and potassium absorption is a manifestation of the more general relation between the anions and cations. These two nutrients are absorbed in larger quantities than the other nutrient ions and it is to be expected, therefore, that an anion:cation balance will depend largely on a nitrogen:potassium balance. The N:K ratio did not, however, remain constant in spite of nitrogen limitation as did the anion:cation ratio, so it may be concluded that the latter is the more

fundamental relationship.

A complete agreement between our results and those of Beckenbach et al (1) is not to be expected as these workers used excesses rather than deficiencies of the nutrients and did not include all possible combinations of the concentration used. The behavior of plants may be different under these conditions. Moreover, the statistical method used by these workers requires the elimination of so many independent variables that the significance of the net regression curves based on sixteen treatments becomes questionable. Unless an analysis of covariance has shown a uniform regression within and between the triplicate cultures, the use of the individual data for calculating the net regression curves cannot be justified. The data presented by these workers do not allow an accurate calculation of the anion:cation ratio, but a study of their results does not indicate that any great variation in this ratio occurred, and it is probable that the forces controlling the anion:cation balance contributed to most if not all of the effects observed by these workers.

CONCLUSION

In the light of the data presented in this thesis it is necessary to modify slightly our suggestion that plants tend to maintain a constant anion:cation balance

within themselves. The anion:cation ratio is maintained when an anion is limited as cation absorption cannot continue independently of anion absorption. When a cation normally absorbed in large quantities is limited the anion: cation ratio increases as anion absorption, though limited to some extent, continues in excess of the cation absorption.

This excess absorption of anions over the absorption of cations is made possible by the exchange of bicarbonate or other negative ions for the nutrient anions. No such ion exchange is possible in the case of the cations, so cation absorption cannot occur in excess of anion absorption. The anion:cation ratio is greater than one in the majority of the cases studied, so a considerable amount of anion exchange must normally occur, but this amount is relatively constant and is only increased when cation absorption is decidedly limited.

SUMMARY

1. Wheat, variety Red Bobs, was grown in culture solutions in which nitrogen and potassium and potassium and calcium were limited. The experiments were adequately replicated.

2. The growth of the plants was decreased by the

limitation of nitrogen and of potassium under the conditions used.

3. Plants grown in the low nitrogen solutions contained more phosphorus and less of each of the other nutrients than did plants grown in complete solutions.

4. When nitrogen and potassium were limited, the plants grown in low potassium solutions contained more calcium and less of each of the other nutrients than did plants from complete solutions.

5. When potassium and calcium were limited, the plants grown in low potassium solutions contained less of each of the nutrients except calcium and magnesium than did the plants grown in complete solutions. These two elements were absorbed in approximately equal amounts by plants in the complete and low potassium solutions in spite of the reduced growth when potassium was limiting.

6. Plants grown in the low calcium solutions contained more magnesium, similar amounts of potassium, and sulphur, and less of the other nutrients than did the plants grown in complete solutions.

7. Neither the limitation of nitrogen nor of calcium affected the anion:cation ratio within the plants. The limitation of potassium did significantly affect this ratio although the decreased absorption of potassium was

partly offset by the increased absorption of calcium and the decreased absorption of nitrogen.

8. It is suggested that this failure to maintain the constant anion:cation balance when potassium was limited may be due to the ability of the plant to absorb anions by ionic exchange, the bicarbonate ion being especially significant in this regard.

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